Pedobiologia **26**, 331—347 (1984)

Department of Biology, University of Calgary
Calgary, Alberta, Canada

Population dynamics and production studies of *Phryganella acropodia* and *Difflugiella oviformis* (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil

J. Daniel Lousier

With 7 figures

(Accepted: 83-06-11)

1. Introduction

While soil Testacea can be identified as a major component of the soil protozoan fauna in some soils, little is known regarding their population ecology. For example, poorly known aspects of testacean ecology are annual population dynamics, secondary production, biomass turnover and impact on the organic cycle. The Euglyphidae have been the object of most of the interest with regard to such study (Smith 1973; Lousier 1974a, b; Schönborn 1975, 1977, 1978, 1982; Coûteaux 1976, 1978; Laminger 1978; Laminger *et al.* 1980). A small amount of information is available for the Nebelidae and Centropyxidae as well (Lousier 1974b; Schönborn 1977, 1978; Coûteaux 1978; Laminger *et al.* 1980; Foissner & Adam 1981).

Phryganella acropodia and *Difflugiella oviformis* are small, ubiquitous and abundant Testacea but because of their size may not have a significant impact on the organic cycle. While little basic biological or taxonomic data are available, Schönborn (1977) has provided estimates of annual production, number of generations per year and daily mortality rate for *P. acropodia* in forest floor moss. Laminger *et al.* (1980) considered *Phryganella* as a numerically dominant genus throughout the year in some subalpine soils and Schönborn (1978) provided a 3 month estimate of the production of *P. acropodia* in a beechwood soil. There is no population ecology information available for *D. oviformis*. Deflandre (1953), Grospietsch (1964) and Page (1966) provided taxonomic reviews of the genus and Bonnet & Thomas (1960) have summarized the known geographical distribution of the species. Griffin (1972) described some basic biological phenomena, e.g., movement, fine structure and fusion of pseudopods and test ultrastructure for a species of *Difflugiella*. Hedley *et al.* (1977) detailed test and cellular ultrastructure, reproduction, pseudopodia structure and generation time (culture) for *Cryptodifflugia oviformis* Penard 1890 [≙ *D. oviformis*].

The objectives of this paper are: (1) to detail the annual variation in total population density, biomass, production and turnover for both species in each soil and litter layer; (2) to quantify the relationship of the species to the total testacean community; and (3) to assess the relative importance of the species in the aspen woodland soil. The investigation was carried out in a cool temperate deciduous woodland for 57 weeks and also involved similar studies for the Centropyxidae (Lousier 1984a), the Euglyphidae (Lousier 1984b), and the Nebelidae (1984c).

2. Site and methods

2.1. Site location and description

The general study area was located at the northern end of the Kananaskis Valley (115° 00′—115° 06′ W, 51° 00′—51° 04′ N) in the Fisher Range of the Rocky Mountains of Alberta, Canada, and encompassed about 21 km². Kirby (1973) has provided a general description of the northern

Table 1. Description of the soil organic layers in the aspen woodland

Horizon Depth *p*H	Description
L 0—2 cm 6.4	Distinct litter of leaves (aspen, herb, grass), petioles and wood material; some leaves near bottom exhibit fenestration; fungal mycelia, few faecal pellets present; few pine and spruce needles; compact layer.
F 2—4 cm 6.4	Smaller litter fragments; large degree of fenestration; much fungal mycelia and many faecal pellets; a few roots present.
H 4—6 cm 6.6	Amorphous, greyish-black, finely divided organic material; occasional litter fragment; abundant mycelia, faecal pellets and roots; occasional small stones.
Ah 6—7 cm 6.7	Transition of humus to mineral layer; amorphous, very finely divided organic matter mixed with mineral materials; more visible root and mycelial material than A_0H; greyish-black; a few small stones.
A 7 cm 6.7	Greyish-brown, crumbly mineral material; many small stones; many larger roots present; material much drier than A_0H or Ah.

part of the Kananaskis Valley, including descriptions of the climate, physiography, hydrology, geology, soils and forest inventory. KARKANSIS (1972) surveyed the soils of the entire valley and LOUSIER (1974a, 1975) described the organic layers of several valley soils, including the aspen woodland soil. The vegetation of the main aspen site has been detailed by DENNIS (1970).

The site was an aspen woodland located 1,400 m ASL on a well-drained, south-facing slope at the northern end of the Kananaskis Valley in the Rocky mountains of Alberta, Canada. The climate is essentially continental, characterized by short, dry summers and relatively long, cold winters with intermittent, warm, chinook winds. The soil has been classified in the orthic gray luvisol subgroup, and has a surface organic horizon (mor humus) easily separated into L (whole litter), F (fragmented litter), H (humus) and Ah (black mineral) layers (Table 1). The canopy was dominated by trembling aspen (*Populus tremuloides* MICHX.), with balsam poplar (*P. balsamifera* L.) being less frequent in occurrence. Various grasses, herbs and wild rose shrubs were the main components of the understory. Additional, detailed information on the soil, vegetation, meteorology, litter input, litter decomposition, and litter and soil chemistry of the study site is available in CRAGG *et al.* (1977), DENNIS (1970), LOUSIER (1974a, 1975, 1976), and LOUSIER & PARKINSON (1976, 1978, 1979).

Precipitation during the period of non-frozen soil in the sample plots, measured at weekly intervals, is illustrated in Fig. 1. This precipitation is water that should affect soil moisture content directly and thus have greater biological significance. Soil temperatures were measured at three depths: 0.5—1.5 cm (L layer), 3.0—4.0 cm (F layer) and 5.0—6.0 cm (H layer), in the study plots, and the seasonal and annual variations are given in Fig. 2. Soil moisture contents were measured for the four layers, L, F, H and Ah, and are illustrated in Fig. 3.

2.2. Arrangement of study plots

The study plots were located in the main study site (LOUSIER & PARKINSON 1976, p. 420), and the arrangement of the plots is shown in Fig. 4. Each subplot (i.e., subplots 1, 2, 3, ... 50) was 1 m × 1 m and each linear group of 5 consecutive subplots (e.g., 1—5, 11—15, 36—40) was separated from the adjacent groups of subplots by a 1 m wide buffer area used primarily as a pathway. The location of the meteorological equipment, the coordinates of the plots, and the areas under open or closed canopy are given in Fig. 4.

2.3. Methods

2.3.1. *Sampling program*

In line with the conclusions derived in LOUSIER & PARKINSON (1981a), a sample size of 20 soil cores was adopted. Sampling frequency was weekly because LOUSIER (1974a) found field turnover times for Testacea in the range of 6—10 days and COÛTEAUX' (1976) studies also suggested weekly sampling. At each sampling time, 20 separate subplots were chosen from the main study plot (Fig. 4), using a table of random numbers. A pair of sample cores was taken from each subplot as shown in Fig. 5, i.e., one sample core in the northeast quadrant and one in the southwest quadrant, giving a total of 40 cores, each 8—10 cm deep and having a top surface area of 9.6 cm². No subplot was sampled twice (i.e., two pairs of sample cores at any one sampling time), and the coordinates of each sample core taken were eliminated from the random number selected for coordinates of future samples.

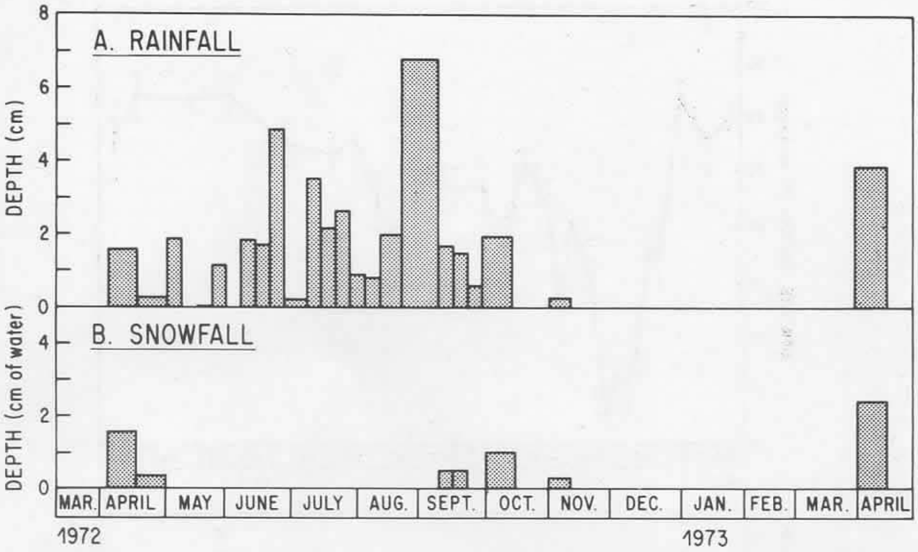


Fig. 1. The rainfall (A) and snowfall (B) during the seasons of unfrozen soil in the aspen woodland during the study period.

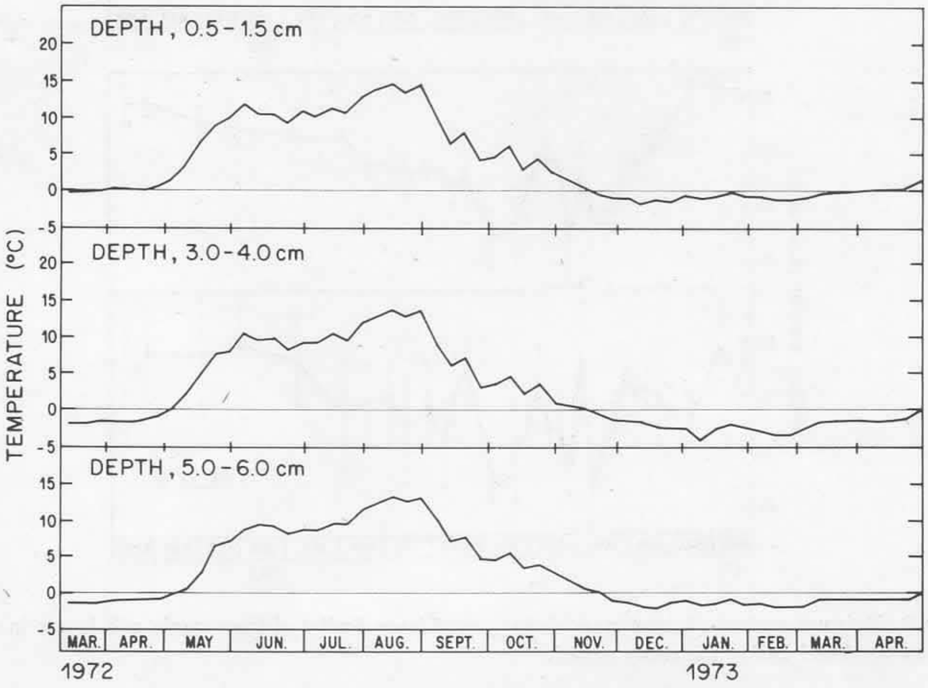


Fig. 2. Soil temperatures at three depths below the forest floor surface in the aspen woodland during the study period.

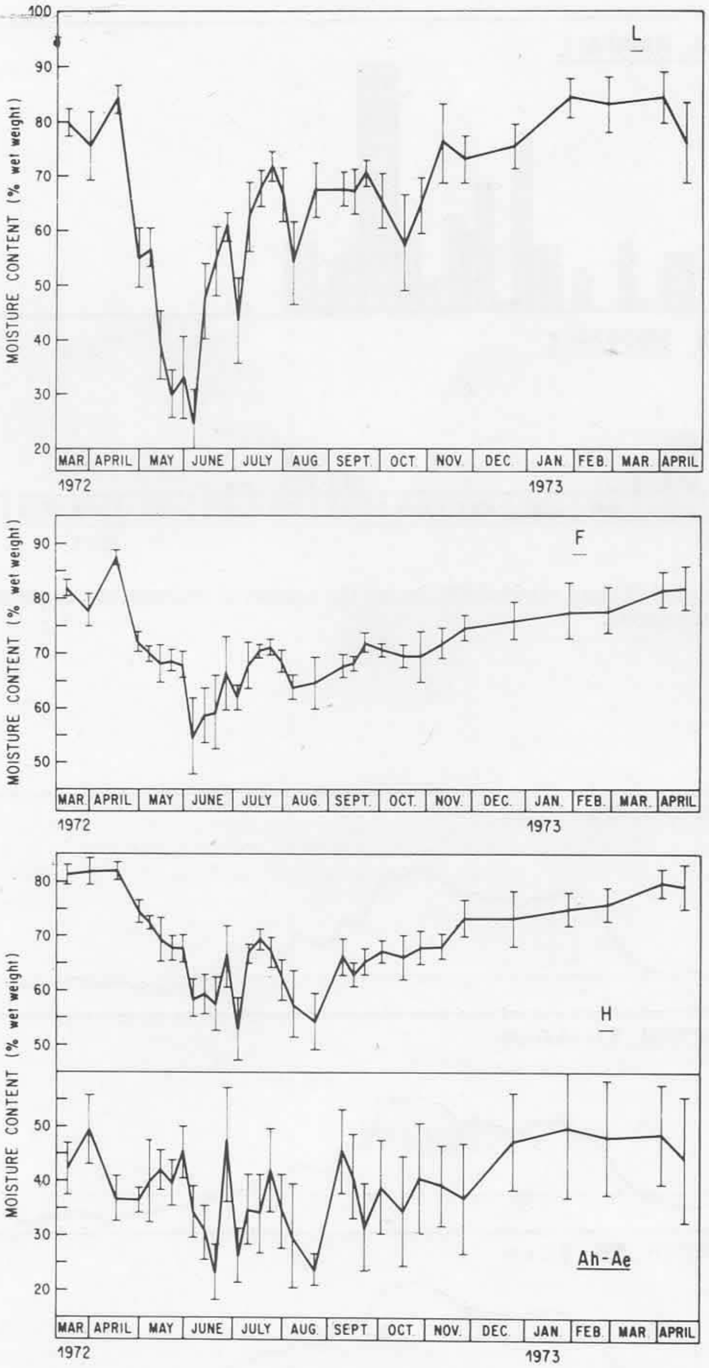


Fig. 3. Moisture content (% wet mass ± 95% confidence limits) of the organic soil layers in the aspen woodland during the study period.

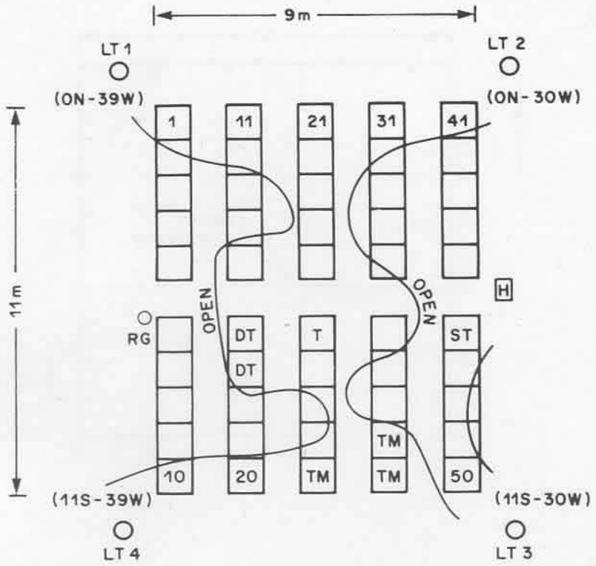


Fig. 4. The arrangement of the main study plot in the aspen woodland (LT, litter trap; RG, rain gauge; DT, soil temperature probes; TM, soil temperature and moisture probes; T, subplot completely treed; ST, stump; H, air hygrothermograph; (ON-39W), staked coordinates of the master grid for the aspen site; OPEN, open canopy (the rest of the area is closed canopy).

2.3.2. Sample preparation and handling

Only one core of each pair of soil cores was used for population density estimates, the other core being used for chemical analysis. Each of the 20 cores used for the population studies was split into its constituent layers (L, F, H, Ah), and 1 g subsamples (wet mass) were taken from each layer, fixed in 20—30 ml of Bouin-Hollande solution for 12 h and then stained with 5 ml of 1% xylidine de ponceau for 1 h. After the staining period, the subsamples were macerated for 10 sec at 3000 rpm in a blender. The suspension was diluted to 1 litre with distilled water, and then agitated manually while an aliquot (L, F, H — 10 ml, Ah — 5 ml) was taken. The aliquot (representing 5 or 10 mg of wet soil) was filtered through a millipore filter apparatus, the filters being 25 mm in diameter (type HAWP 02500) and having a pore size of 0.45 μm. The filter, containing all the suspended material in the aliquot, was then airdried for 1 h, cleared in xylene and mounted in Canada balsam on a microscope slide. The slide was then examined in total under phase contrast microscopy (at ×250; species identity was verified under ×400 if so required), and the Testacea encountered were identified and counted as empty tests, active cells or encysted forms. Soil sample mass and moisture content determinations were made gravimetrically on the cores used for chemical analysis.

2.3.3. Population analysis

The following formulae were used for the calculation of the various population statistics:

(1) tests eliminated (a_8 — Lousier 1974a; Lousier & Parkinson 1981b)

$$a_8 = (E)(T_0)$$

where a_8 = number of tests eliminated; E = rate of test disappearance (%), and T_0 = number of empty tests at the beginning of time t. (E was estimated from the data in Lousier & Parkinson 1981b).

(2) production numbers (P_N)

$$P_N = N_t - N_0 + (T_t - T_0 + a_8)$$

where P_N = number of discrete individuals produced, N_0 = number of live individuals at the beginning of t, N_t = number of live individuals at end of t, T_t = number of empty tests at time t.

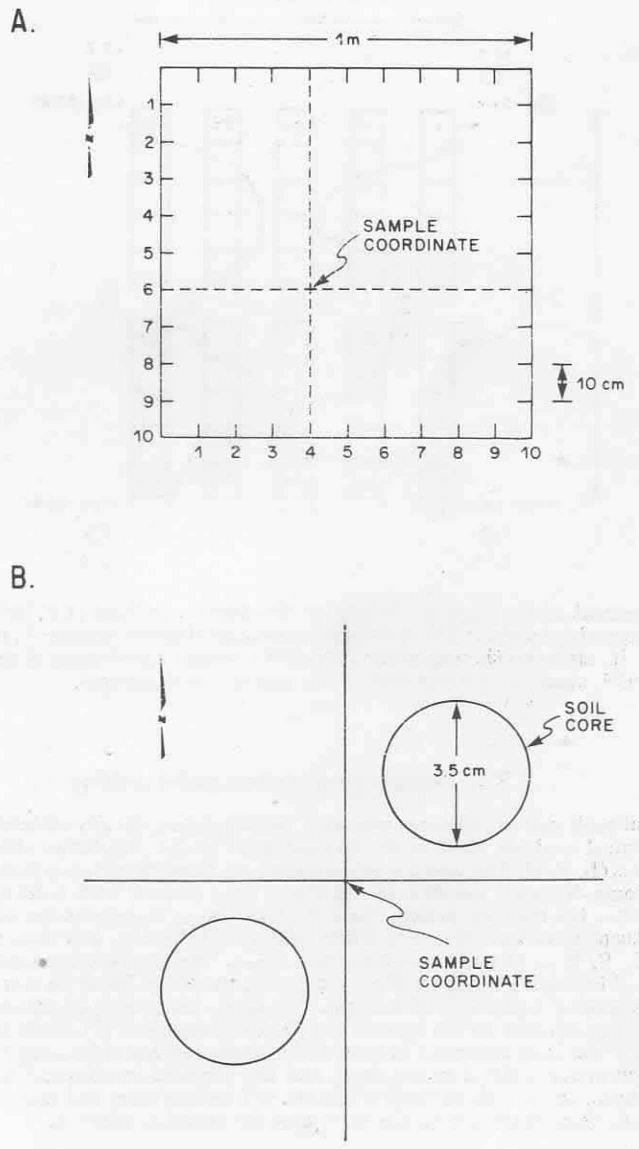


Fig. 5. (A) The arrangement of one subplot in the main study plot in the aspen woodland; (B) Location of the soil cores about the sample co-ordinate in a subplot.

(3) intrinsic rate of natural increase (r)

Using $N_t = N_0 e^{rt}$ (Birch 1948), N_t can be considered cumulative in time (Petrusewicz & MacFadyen 1970) and can be replaced by P_N. Consequently,

$$r = \frac{\ln P_N - \ln N_0}{t}$$

where r = the intrinsic rate of natural increase of the population (number of discrete individuals produced per discrete individual per unit time).

(4) generation time (T) and number of generations per year (G)

$$T = \frac{\ln 2}{r} = 0.693/r$$

where T = generation time, and

$$G = \sum_{i=1}^{52} 7/T$$

G = number of generations produced per year.

(5) mortality (M)

$$M = \left[\frac{\frac{\text{number of tests eliminated during t}}{\text{number of tests living during t}}}{t}\right] \cdot 100\%$$

$$M = \left[\frac{\frac{T_t - T_0 + a_8}{T_t - T_0 + a_c + N_t}}{t}\right] \cdot 100\%$$

where M — percentage of the number of discrete individuals lost during t.

(6) secondary production (P_B)

$$P_B = (P_N)(B)$$

where P_B = the biomass of the number of discrete individuals produced during t, and B = biomass per cell of the species, and P_B/B = biomass turnover rate where B = mean annual standing crop of a species.

The studies presented here are the first attempt to incorporate a detailed estimate of test disappearance rates in the calculation of production numbers. From the results of LOUSIER & PARKINSON (1981b), a static, experimental disappearance rate was applied to dynamic field populations. Consequently, all moisture contents above 60% (wet) in a layer were assumed to have only one test disappearance rate for each species, all moisture contents between 40% and 60% in a layer only one disappearance rate for each species, etc. Thus, for example, each of the F and H layers, having moisture contents near or above 60% throughout the study period, had one test disappearance rate used for each species for the entire year, even in winter when the Testacea were still active.

3. Results

3.0. General

The species *P. acropodia* and *D. oviformis* were observed as living and active in all layers of the aspen woodland soil and were also recorded as constant species (Table 2). The cell biomass measured for each species (Table 2) did not vary seasonally or spatially and compared

Table 2. Occurrence, distribution, biomass (mg 10^{-6} cells) and constancy of *Phryganella acropodia* and *Difflugiella oviformis* in the organic layers of the aspen woodland soil

Species observed	Biomass	No. of cells measured	Distribution				Constancy (%)c)			
			L	F	H	Ah	L	F	H	Ah
Phryganella acropodia (HERTWIG et LESSER) HOPKINSON	4.2 ± 0.3a)	100	b) +/+	+/+	+/+	+/+	100	100	100	90
Difflugiella oviformis (PENARD) BONNET and THOMAS	0.5 ± 0.004	100	+/+	+/+	+/+	+/+	100	100	100	100

a) — Standard error

b) — Observed as living/observed as empty tests

c) — Constancy: Species observed in > 50% of samples — constant in frequency;
Species observed in 25—50% of samples — incidential in frequency;
Species observed in < 25% of samples — accidental in frequency (COÛTEAUX 1976)

favourably with the estimates given in Schönborn (1977, 1978). However, the biomass for *P. acropodia* in a mull humus was 5 times greater. Estimates of the live mass of an individual cell were made by calculating the volume of the cell and assuming a specific gravity of about 1.0 (Heal 1970). The estimates were made primarily on live individuals isolated from field samples with some augmentation with measurements from the Coûteaux slides. *D. oviformis* was recorded as 1 of the 2 initial colonizing species in decomposing aspen and balsam poplar litter and increased in biomass with the age of litter (Lousier 1982). *P. acropodia* appeared in the litter 10 months after the initiation of decomposition and also increased in biomass with litter age (Lousier 1982). This pattern fits with the increase in biomass with profile depth for both species (Tables 3, 4).

3.1. *Phryganella acropodia*

The annual fluctuations of active *P. acropodia* in each layer were similar in pattern, characterized by mid-summer, post-leaf fall and winter peaks (Fig. 6). There is some evidence of an inverse relationship between cyst numbers and numbers of active forms. *P. acropodia* had its highest number of generations in the H layer (Table 3), one of only four species to do so. Along with *T. enchelys*, it was one of the two species to have its highest P_B/B in the H layer; all the other species had their highest P_B/B in the F layer. *P. acropodia* had the third highest H-layer P_B/B of all the species, behind that for *T. enchelys* and *E. laevis*. *P. acropodia* was one of the four species which had sediment-type tests, all of which had nearly the same biomass, but of the four, *P. acropodia* had the highest abundance and turnover rates.

The r, P_B and P_B/B for this species in the F and H layers all showed no seasonal trends, i.e. peaks were recorded in all seasons; in the L layer, peaks were noted only in fall and late winter; in the Ah layer, maximum r values were recorded in summer, fall and late winter, P_B peaked in all seasons, and P_B/B reached its highest levels in summer and fall. The fastest generations observed were: L — 1.4 days (late February), F — 1.0 day (mid-September), H — 1.0 day (mid-September, mid-October), and Ah — 1.1 days (mid-October).

3.2. *Difflugiella oviformis*

The graphs illustrating the population fluctuations for *D. oviformis* (Fig. 7) were similar to those for *E. laevis* and *E. rotunda* (Lousier 1984b), indicating perhaps a response of all three species to similar, if not the same, factors. There are obvious differences in magnitude but the patterns were similar. Intrinsic rates of natural increase were highest in all seasons but winter in the L and Ah layers and showed no seasonal trends at all in the F and H layers. Production biomass peaked in all seasons in the F, H and Ah layers and in all but winter in the L layer, while production biomass turnover rates peaked in the spring in the L layer, in all seasons in the F, in the spring and summer in the H and in spring, summer and fall in the Ah layer. The fastest generation times recorded were: L — 0.9 day (early June), F — 1.1 days (mid-May), H — 1.3 days (mid-July), and Ah — 1.1 days (late June). *D. oviformis* was the only species to have its highest P_B/B in the L layer (Table 4).

In comparison with the other species, *D. oviformis* had by far the highest mean annual density and total annual production numbers in all layers but was amongst the lowest species in terms of mean annual biomass and total annual production biomass. With regard to mean annual intrinsic rate of natural increase, total annual number of generations, and mean annual weekly production biomass turnover, *D. oviformis* ranked ahead of all other species in the L and Ah layers. It appeared that this species may have been the most successful of all the testacean species encountered because of its high turnover rates in the two layers less preferred by most other species (L and Ah).

4. Discussion

The information in Fig. 6 and 7 can be summarized with some general comments. The patterns for the population fluctuations were very similar for *P. acropodia* in each of the 4 organic layers. The same was so for the Centropyxidae (Lousier 1984a) and the Nebelidae

Table 3. Summary of the population parameters calculated for *Phryganella acropodia*

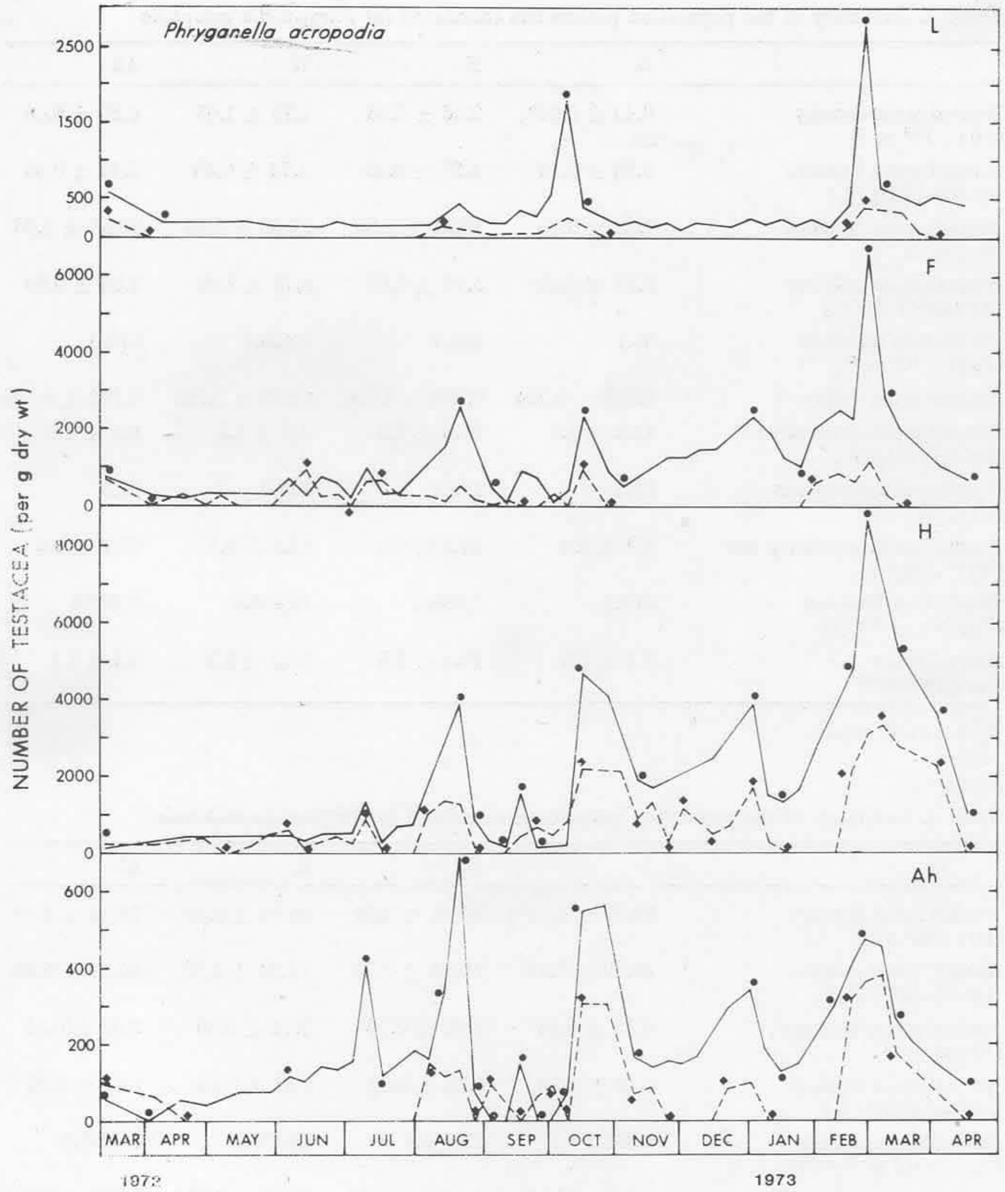
	L	F	H	Ah
Annual mean density (D) ($\times 10^6$ m^{-2})	0.40 ± 0.07*)	2.56 ± 0.33	7.79 ± 1.09	0.80 ± 0.09
Annual mean relative density (RD) (%)	3.66 ± 0.77	4.23 ± 0.35	4.74 ± 0.45	5.45 ± 0.63
Annual mean biomass (B) (mg m^{-2})	1.59 ± 0.28	10.81 ± 1.39	27.66 ± 3.62	10.53 ± 1.36
Annual mean relative biomass (RB) (%)	3.46 ± 0.52	5.74 ± 0.63	8.78 ± 1.02	9.06 ± 0.80
Production numbers (P_N) ($\times 10^6$ m^{-2} y^{-1})	66.1	806.7	2,426.1	578.0
Annual mean r (day^{-1})	0.121 ± 0.014	0.238 ± 0.024	0.270 ± 0.020	0.182 ± 0.015
Annual mean generation time (T) (days)	11.2 ± 1.7	10.0 ± 3.0	4.8 ± 1.3	6.1 ± 1.0
Number of generations (G) (y^{-1})	57.8	113.1	129.3	87.0
Annual mean mortality rate (M) (% day^{-1})	8.9 ± 0.3	11.5 ± 0.3	12.3 ± 0.1	10.7 ± 0.2
Production biomass (P_B) (mg m^{-2} y^{-1})	277.2	3,388.2	10,189.6	2,427.8
Annual mean P_B/B (week^{-1})	3.2 ± 0.5	10.0 ± 2.6	10.0 ± 2.5	5.5 ± 1.5

*) standard error

Table 4. Summary of the population parameters calculated for *Difflugiella oviformis*

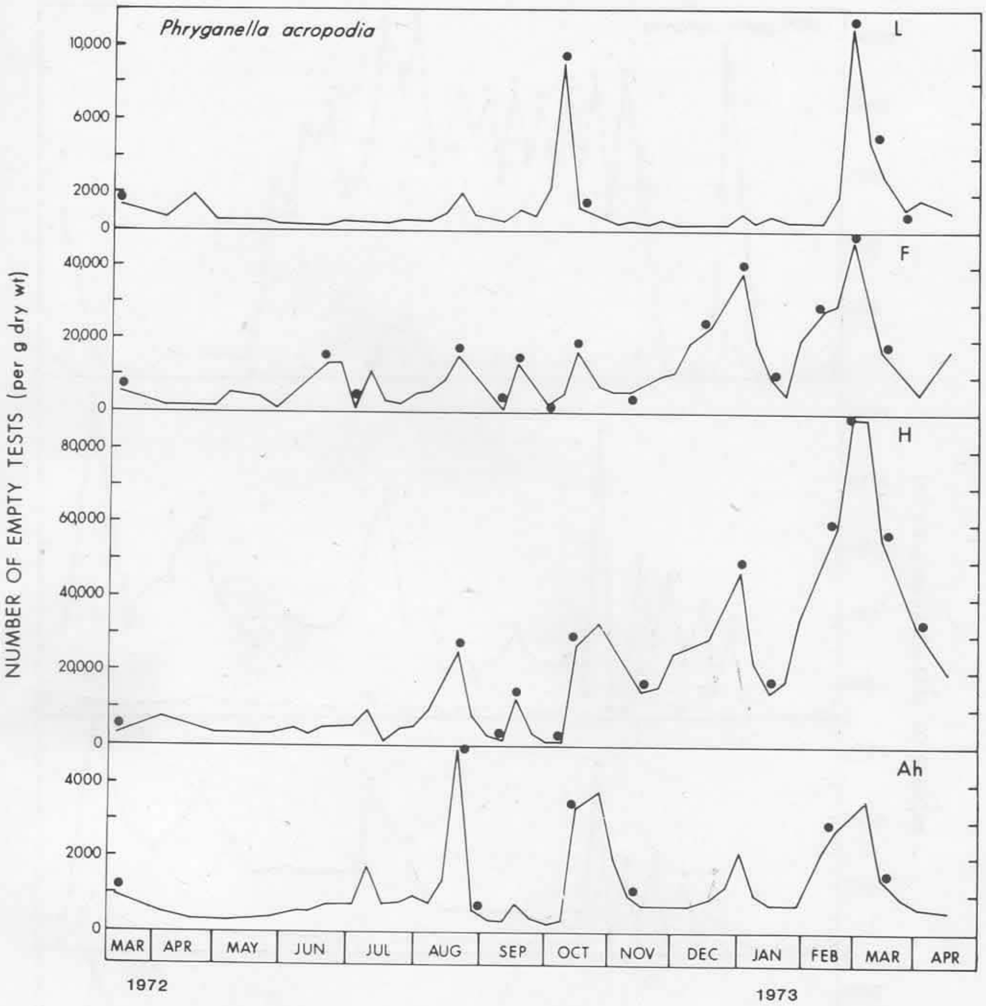
	L	F	H	Ah
Annual mean density (D) ($\times 10^6$ m^{-2})	10.27 ± 1.11*)	31.34 ± 2.86	86.95 ± 8.58	13.46 ± 2.19
Annual mean relative density (RD) (%)	49.69 ± 3.59	50.98 ± 2.19	54.24 ± 2.58	55.22 ± 2.98
Annual mean biomass (B) (mg m^{-2})	0.52 ± 0.06	1.61 ± 0.17	3.74 ± 0.36	2.02 ± 0.34
Annual mean relative biomass (RB) (%)	1.22 ± 0.15	0.86 ± 0.08	1.29 ± 0.13	1.61 ± 0.20
Production numbers (P_N) ($\times 10^6$ m^{-2} y^{-1})	3,348.2	10,442.4	19,380.1	18,801.8
Annual mean r (day^{-1})	0.228 ± 0.018	0.263 ± 0.017	0.248 ± 0.016	0.259 ± 0.020
Annual mean generation time (T) (days)	4.7 ± 0.58	3.4 ± 0.31	4.1 ± 0.70	6.8 ± 2.44
Number of generations (G) (y^{-1})	108.4	125.6	117.7	122.9
Annual mean mortality rate (M) (% day^{-1})	11.6 ± 0.22	12.2 ± 0.12	11.9 ± 0.14	12.0 ± 0.16
Production biomass (P_B) (mg m^{-2} y^{-1})	167.4	522.1	969.0	940.1
Annual mean P_B/B (week^{-1})	16.2 ± 6.5	12.0 ± 2.1	7.1 ± 0.8	10.2 ± 1.8

*) standard error



6 A

(Lousier 1984c). For *D. oviformis*, however, the pattern in the L layer was quite distinct from that in the F, H and Ah layers, a situation similar to that for the Euglyphidae (Lousier 1984b). Both species had a major peak in abundance in the autumn in each layer, the peak occurring just before the onset of frozen conditions. In the F, H and Ah layers, both species maintained abundant, active (reproducing) populations over the winter period. *P. acropodia* numbers in the L layer were low and fairly stable over the winter until the end of February when the annual maximum abundance was reached. The L layer abundance of *D. oviformis* decreased over the winter until the beginning of spring thaw. *P. acropodia* reached maximum abundance in the winter in the L, F and H layers while *D. oviformis* did the same in the F,

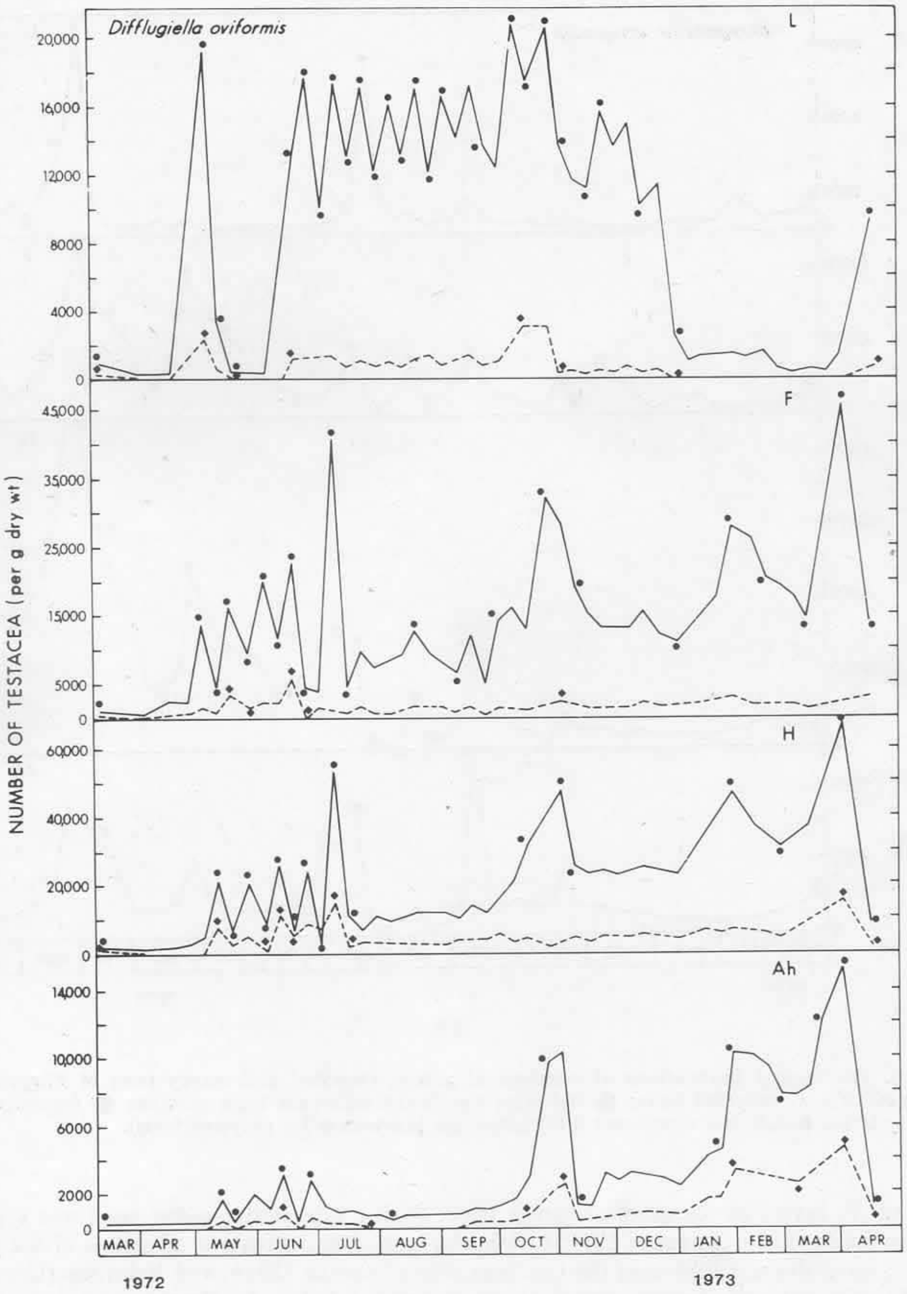


6 B

Fig. 6. The annual fluctuations of numbers of active, encysted and empty tests of *Phryganella acropodia* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).

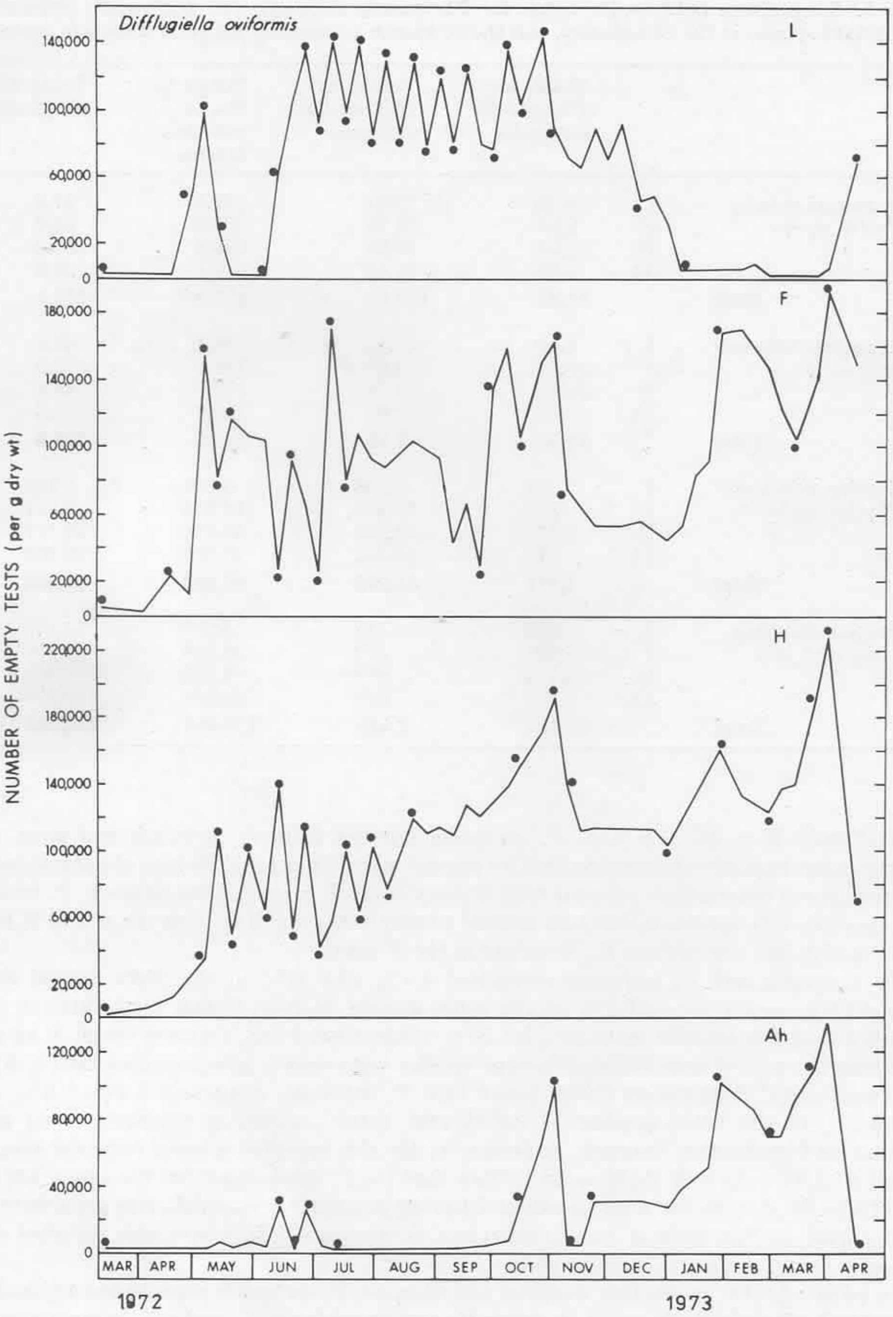
H and Ah layers at the onset of spring thaw. Such a late winter-spring peak was typical of the Euglyphidae (Lousier 1984b) while the lack of an increase at this time of the year for *P. acropodia* was typical of the Centropyxidae (Lousier 1984a) and Nebelidae (Lousier 1984c). The patterns of empty test fluctuations paralleled those for the active forms for both species. The variations in cyst numbers when the cysts were recorded, generally paralleled the fluctuations of active forms, i.e., coincident increases and decreases. Cysts were observed in low numbers generally throughout most of the year for *D. oviformis*, the only such situation among all the species observed.

The annual mean weekly density and biomass of both species increased with profile depth to the H layer, being ranked H > F > Ah > L except for biomass for *D. oviformis* which was ranked H > Ah > F > L. While the highest production (numbers and biomass) was recorded in the H layer for both species, the rankings differed: *P. acropodia*, H > F > Ah > L;



7A

Fig. 7. The annual fluctuations of numbers of active, encysted and empty tests of *Difflugiella oviformis* (----- encysted tests; ● indicates significant difference from previous ● for active or empty tests; ◆ indicates significant difference from previous ◆ for encysted tests).


Difflugiella oviformis
L
F
H
Ah
NUMBER OF EMPTY TESTS (per g dry wt)
140,000
100,000
60,000
20,000
0
180,000
140,000
100,000
60,000
20,000
0
220,000
180,000
140,000
100,000
60,000
20,000
0
120,000
80,000
40,000
0
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
1972
1973

7 B

Table 5. Comparisons between the totals for *Phryganella acropodia* and *Difflugiella oviformis*, the 14 constant species in the community, and the 28 species comprising the total testacean community

		Totals for *Phryganella acropodia*	Totals for *Difflugiella oviformis*	Totals for the 14 constant species	Totals for all 28 species
Mean annual density (D) ($\times 10^6$ m^{-2})	L	0.40	10.27	17.3	17.8
	F	2.56	31.34	62.0	64.0
	H	7.79	86.95	156.4	158.0
	Ah	0.80	13.46	20.1	20.9
Total		**11.45**	**142.02**	**255.8**	**260.7**
Mean annual biomass (B) (mg m^{-2})	L	1.59	0.52	36.1	46.2
	F	10.81	1.61	148.0	210.0
	H	27.66	3.74	275.8	346.1
	Ah	10.53	2.02	118.6	120.6
Total		**50.56**	**7.89**	**578.6**	**722.9**
Production numbers (P_N) ($\times 10^6$ m^{-2} y^{-1})	L	66	3,348	5,034	5,190
	F	807	10,442	19,850	20,677
	H	2,426	19,380	37,052	38,197
	Ah	578	18,802	25,056	26,862
Total		**3,877**	**51,972**	**86,992**	**90,926**
Production Biomass (P_B) (mg m^{-2} y^{-1})	L	277	167	8,295	14,479
	F	3,388	522	48,158	59,950
	H	10,190	969	91,428	100,995
	Ah	2,428	940	30,504	31,107
Total		**16,283**	**2,598**	**178,385**	**206,531**

D. oviformis, H > Ah > F > L. *P. acropodia* differed from *D. oviformis* and most of the other constant species observed in that its annual mean daily intrinsic rate of natural increase and number of generations per year were highest in the L layer instead of the F. *P. acropodia* was also the only species to have its annual weekly mean P_B/B in both the F and H layers; most species had the highest P_B/B values in the F layer.

P. acropodia and *D. oviformis* comprised 4.4% and 54% of the mean annual density respectively, and 7.2% and 1% of the mean annual biomass (Table 5). Laminger (1978) reported that *Phryganella* accounted for 10% of the total living Testacea found in an alpine brown-earths podsol and *Difflugiella*-type species were only a minor component (< 3%) of the community. Schönborn (1982) found that *P. acropodia* comprised 7.4%, 5.9%, 4.9% and 4.3% of the total number of individuals, total production numbers, mean annual biomass and production biomass, respectively. He also reported a lower turnover rate, e.g., $M = 1.8\%$, $G = 14\ y^{-1}$, $P_B/B = 22.1$, than that for *P. acropodia* from the aspen woodland soil (Table 3), despite his mull population having generally a much shorter generation time ($T = 4.2$ days). Foissner & Adam (1981) and Schönborn (1977) have also reported slower turnover for *P. acropodia* in other soils.

In terms of total production numbers and biomass, *P. acropodia* represented 4% and 8%, respectively, in this study while *D. oviformis* accounted for 57% and 1%, respectively. The total annual production for *P. acropodia* in this study (16.3 g m^{-2}) far exceeded the total for this species of 3.2 mg m^{-2} in a beechwood moss cushion (Schönborn 1977), 2.3 g m^{-2} for a beechwood soil (Schönborn 1978), and 1.1 g m^{-2} for an ash-maple soil (mull humus) (Schönborn 1982). No such comparable information is available for *D. oviformis*.

After estimating annual secondary production, it is possible to calculate the approximate amount of food consumed by the testacean populations (Heal 1967; Laybourn 1976) (Table 6). The estimates for amount of food consumed per year accounted for 8% and 1%

Table 6. Energy budget for *Phryganella acropodia* and *Difflugiella oviformis* in the aspen woodland soil

		P. acropodia	*D. oviformis*
Mean annual biomass, B ($\times 10^{-3}$)	L	1.6	0.5
	F	10.8	1.6
	H	27.7	3.7
	Ah	10.5	2.0
Total		**50.5**	**7.8**
Total annual production, P_B	L	0.28	0.17
	F	3.39	0.52
	H	10.19	0.97
	Ah	2.43	0.94
Total		**16.29**	**2.60**
Total annual respiration losses, R	L	[a]) 0.5 (0.1)[b])	0.3 (0.1)
	F	5.7 (1.7)	0.8 (0.3)
	H	17.0 (5.1)	1.6 (0.5)
	Ah	4.1 (1.2)	1.6 (0.5)
Total		**27.3 (8.1)**	**4.3 (1.4)**
Total annual egestion losses, E	L	1.1 (0.3)	0.7 (0.2)
	F	13.6 (3.4)	2.1 (0.5)
	H	40.7 (10.2)	4.0 (1.0)
	Ah	9.7 (2.4)	3.8 (0.9)
Total		**65.1 (16.3)**	**10.6 (2.6)**
Total annual ingestion, I	L	1.9 (0.7)	1.1 (0.4)
	F	22.6 (8.5)	3.5 (1.3)
	H	67.9 (25.5)	6.5 (2.4)
	Ah	16.2 (6.1)	6.3 (2.4)
Total		**108.6 (40.8)**	**17.4 (6.5)**

[a]) Values not in parentheses represent 10 °C, where $P = 0.15\ I$, $R = 0.25\ I$ and $E = 0.60\ I$ (ROGERSON 1981).

[b]) Values in parentheses represent optimum temperatures (15—25 °C), where $P_B = 0.4\ I$, $R = 0.25\ I$, and $E = 0.4\ I$ (HEAL 1967, LAYBOURN 1976).

Note: All estimates are wet biomass, g m^{-2}.

of the total consumption by all Testacea for *P. acropodia* and *D. oviformis* respectively. The amount ingested by *P. acropodia* comprised almost twice the annual mean standing crop of bacteria. P_B/B for *P. acropodia* averaged 260 (range, 140—365) for all layers, while *D. oviformis* averaged 330 (range, 240—470). The amount of carbon respired per year was estimated as: *P. acropodia* — 2.73 g m^{-2} (dry mass) $\times 47\%$ (C content of amoebae, BAND 1959) $= 1.3$ g m^{-2}; *D. oviformis* — 0.43 g $m^{-2} \times 47\% = 0.2$ g m^{-2}. This amounted 0.5% and 0.07% of the total annual carbon input to the soil system for *P. acropodia* and *D. oviformis* respectively. The respiration losses represented 8% and 1.3% of the total testacean respiration losses for *P. acropodia* and *D. oviformis*, suggesting minor roles for these species in the aspen woodland organic cycle. The 8% loss by *P. acropodia* was less than 1/2 that for the Centropyxidae (LOUSIER 1984a) and was 1/8 that for the Euglyphidae (LOUSIER 1984b).

5. Acknowledgements

Financial support for the study was provided by NSERC Operating Grant (No. A2257) to Dr. DENNIS PARKINSON and an NRCC Postgraduate Scholarship to the author.

6. References

Band, R. N., 1959. Nutritional and related biological studies on the free-living soil amoeba, *Hartmannella rhysodes*. J. Gen. Microbiol. **21**, 80—95.

Birch, L. C., 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. **17**, 15—26.

Bonnet, L., & R. Thomas, 1960. Faune terrestre d'eau douce des Pyrénées Orientéles. 5. Thécamoebiens du sol. Hermann edit. Paris, 1—104.

Coûteaux, M.-M., 1976. Dynamisme de l'équilibre des Thécamoebiens dans quelques sols climaciques. Mém. Mus. Nat. Hist. Nat. N. S. ser. A. Zoologie **96**, 1—183.

— 1978. Étude quantitative des Thécamoebiens dans une savane à *Loudetia* à Lamto (Côte d'Ivoire). Rev. Ecol. Biol. Sol **15**, 401—412.

Cragg, J. B., A. Carter, C. Leischner, E. B. Peterson & G. N. Sykes, 1977. Litterfall and chemical cycling in an aspen (*Populus tremuloides* Michx.) woodland ecosystem in the Canadian Rockies. Pedobiologia **17**, 428—443.

Deflandre, G., 1953. Ordres des Testacealobosa, Testaceafilosa, Thalamia ou Thécamoebiens (Rhizopoda Testacea). pp. 97—148. In: P. Grassé (éd.), Traité de Zoologie. Masson, Paris.

Dennis, J. G., 1970. Aboveground accretion of vegetative and reproductive structures in an aspen understory vegetation in southwestern Alberta. Bull. Ecol. Soc. Amer. **51**, 31.

Foissner, W., & H. Adam, 1981. Die Gemeinschaftsstruktur und Produktion der terricolen Testaceen (Protozoa, Rhizopoda) in einigen Böden der Österreischischen Zentralalpen (Hohe Tauern, Glocknergebiet). Veröffentlichungen des Österreichischen MAB — Hochgebirgsprogramms **4**, 53—78.

Grospietsch, T., 1964. Die Gattungen *Cryptodifflugia* und *Difflugiella* (Rhizopoda testacea). Zool. Anz. **172**, 243—257.

Griffin, J. L., 1972. Movement, fine structure, and fusion of pseudopods of an enclosed amoeba, *Difflugiella* sp. J. Cell Sci. **10**, 563—583.

Heal, O. W., 1967. Quantitative studies on soil amoebae. In: O. Graff & J. E. Satchell (eds), Progress in Soil biology. pp. 120—126. North-Holland Publ. Co., Amsterdam.

— 1970. Methods of study of soil Protozoa. p. 119—126. In: J. Phillipson (ed.), Methods of study in soil ecology. UNESCO, Paris.

Hedley, R. H., C. G. Ogden & N. J. Mordan, 1977. Biology and fine structure of *Cryptodifflugia oviformis* (Rhizopoda: Protozoa). Bull. Br. Mus. Nat. Hist. (Zool.) **30**, 313—328.

Karkanis, P. G., 1972. Soils of the Kananaskis Valley. Environmental Sciences Centre (Kananaskis), University of Calgary, Res. Rep. No. 1.

Kirby, C. L., 1973. The Kananaskis Forest Experiment Station, Alberta (history, physical features and forest inventory). Inf. Rep. NOR-X-51, N.F.R.C., C.F.S., Environment Canada, Edmonton, Alberta.

Laminger, H., 1978. The effects of soil moisture fluctuations on the testacean species *Trinema enchelys* (Ehrenberg) Leidy in a high mountain brown-earths-podsol and its feeding behaviour. Arch. Protistenk. **120**, 446—454.

— K. Geisler-Moroden, A. Siess, E. Spiss & B. Spiss, 1980. Populationsdynamik terrestrischer Protozoen (Testacea, Rhizopoda) in zentralalpinen Lagen Tirols. I. Untersuchungen subalpiner Böden im Raum Obergurgl (Tirol/Österreich). Arch. Protistenk. **123**, 280—323.

Laybourn, J., 1976. Energy budgets for *Stentor coeruleus* Ehrenberg (Ciliophora). Oecologia (Berlin/West) **22**, 431—437.

Lousier, J. D., 1974a. Effects of experimental soil moisture fluctuations on turnover rates of Testacea. Soil Biol. Biochem. **6**, 19—26.

— 1974b. Response of soil Testacea to soil moisture fluctuations. Soil Biol. Biochem. **6**, 235—239 (Errata — Soil Biol. Biochem. **7**, 185—188).

— 1975. Relationships between distribution of Testacea (Protozoa, Rhizopoda) and the soil habitat. Naturaliste Can. **102**, 57—72.

— 1976. Testate amoebae (Rhizopoda, Testacea) in some Canadian rocky mountain soils. Arch. Protistenk. **118**, 191—201.

— 1982. Colonization of decomposing deciduous leaf litter by Testacea (Protozoa, Rhizopoda): Species succession, abundance and biomass. Oecologia (Berlin/West) **52**, 381—388.

— 1984a. Population dynamics and production studies of species of Centropyxidae (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil. Arch. Protistenk. In press.

— 1984b. Population dynamics and production studies of species of Euglyphidae (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil. Pedobiologia **26**, 309—330.

— 1984c. Population dynamics and production studies of species of Nebelidae (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil. Acta Protozool. In press.

— & D. Parkinson, 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. **54**, 419—436.

— — 1978. Chemical element dynamics in decomposing leaf litter. Can. J. Bot. **56**, 2795—2812.

— — 1979. Organic matter and chemical element dynamics in an aspen woodland soil. Can. J. For. Res. **9**, 449—463.

— — 1981a. Evaluation of a membrane filter technique to count soil and litter Testacea. Soil Biol. Biochem. **13**, 209—215.
— — 1981b. The disappearance of empty tests of litter and soil testate amoebae (Testacea, Rhizopoda, Protozoa). Arch. Protistenk. **124**, 213—236.
— — 1984. Annual population dynamics and production ecology of Testacea (Protozoa, Rhyzopoda) in an aspen woodland soil. Soil Biol. Biochem. In press.
PAGE, F. C., 1966. *Cryptodifflugia operculata* n. sp. (Rhizopodea: Arcellinida, Cryptodifflugiidae) and the status of the genus *Cryptodifflugia*. Trans. Am. Micros. Soc. **85**, 506—515.
PETRUSEWICZ, K., & A. MACFADYEN, 1970. Productivity of terrestrial animals: principles and methods. IBP Handbook No. 13. Blackwell Scientific Publications, Oxford.
SCHÖNBORN, W., 1975. Ermittlung der Jahresproduktion von Boden-Protozoen. I. Euglyphidae (Rhizopoda, Testacea). Pedobiologia **15**, 415—424.
— 1977. Production studies on Protozoa. Oecologia (Berlin/West) **27**, 171—184.
— 1978. Untersuchungen zur Produktion der Boden-Testaceen. Pedobiologia **18**, 373—377.
— 1982. Estimation of annual production of Testacea (Protozoa) in mull and moder (II). Pedobiologia **23**, 383—393.
— 1983. Beziehungen zwischen Produktion, Mortalität und Abundanz terrestrischer Testaceen-Gemeinschaften. Pedobiologia **25**, 403—412.
SMITH, H. G., 1973. The Signy Island terrestrial reference sites: III. Population ecology of *Corythion dubium* (Rhizopoda: Testacida) in Site I. Brit. Antarct. Surv. Bull., Nos. 33/34, 123—135.

Address of the author: Dr. J. DANIEL LOUSIER, Ecology Program, Research Branch, Ministry of Forests, 1450 Government Street, Victoria, British Columbia, Canada V8W 3E7.

Synopsis: *Original scientific paper*

LOUSIER, J. D., 1984. Population dynamics and production studies of *Phryganella acropodia* and *Difflugiella oviformis* (Testacea, Rhizopoda, Protozoa) in an aspen woodland soil. Pedobiologia **26**, 331—347.

Both species were observed as living and active in all layers of the aspen woodland soil at all sampling times. *P. acropodia* accounted for 4.4% and 7% of the mean annual population density and mean annual biomass, respectively and 4% and 8% of the total production numbers and biomass respectively for the total testacean community. *D. oviformis*, while representing 54% and 57% of the mean annual abundance and total production numbers respectively of all Testacea, accounted for only 1% of the mean annual biomass or total secondary production. Mean annual biomass and total annual production for *P. acropodia* were estimated as 0.051 and 16.3 g wet mass m^{-2} respectively, while total annual ingestion, respiration losses and egestion losses were calculated as 109, 27 and 65 g wet mass m^{-2} respectively. For *D. oviformis*, the values were: mean annual biomass 0.0078 g m^{-2}; total annual production 2.6 g m^{-2}; total annual ingestion 17 g m^{-2}; total respiration losses 4 g m^{-2}; and total egestion losses, 11 g m^{-2}. The annual production biomass varied from 140 to 365 (mean 260) times the standing crop in all the soil layers for *P. acropodia* and from 240 to 470 (mean 330) for *D. oviformis*. The dry mass of carbon respired annually was estimated as 1.3 g m^{-2} for *P. acropodia* and 0.2 g m^{-2} for *D. oviformis* which amounted to 0.5% and 0.1% respectively of the total carbon input.

Key words: Protozoa, Testacea, biomass, production, ingestion, egestion, respiration, energy budget, aspen (Populus tremuloides, balsamifera) woodland soil, Canada.